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Barklice (Insecta: Psocodea) from Early Cretaceous resiniferous forests of Iberia (Spanish amber): New Troctomorpha and a possible Psocomorpha

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ABSTRACT

Psocids, commonly known as barklice, are insects belonging to the order Psocodea, together with the parasitic lice. They usually inhabit forest litter or the bark of tree trunks and branches, showing grazing herbivorous or detritivorous feeding habits. The Cretaceous psocid record is diverse, containing more than 70 described species. Here, we present new psocids (Troctomorpha and possible Psocomorpha) from two Spanish amber outcrops, both Albian (Lower Cretaceous): El Soplao and Ariño. We describe the two new species *Azarpsocus anjana* Álvarez-Parra and Nel sp. nov. (Manicapsocidae) and *Burmacompsocus ojancano* Álvarez-Parra and Nel sp. nov. (Compsocidae), and the morphotype Ariño that might belong to Psocomorpha. We discuss the taxonomic placement of the studied specimens and comment on the palaeobiogeography of the Cretaceous psocids. The Cretaceous barklice fauna from Iberia shows more similarities with that from Lebanese (Barremian) and Burmese (Cenomanian) ambers than with that from the palaeogeographically closer French amber (Cenomanian). This finding has been also reported in other insect groups from Spanish amber, and might be the consequence of several factors, such as the palaeoenvironmental conditions of the ecosystems, the palaeogeographical position of the Iberia Island during the latest Jurassic, closer to Gondwana than to Laurasia, and oceanic currents that facilitated or hindered the displacement of insect fauna between continental masses.

1. Introduction

The order Psocodea encompasses barklice, booklice, and parasitic lice, forming part of the acercarian insects (Johnson et al., 2018). The first two are usually known as psocids, which correspond to a paraphyletic group previously known as ‘Psocoptera’ (Smithers, 1972; de Moya et al., 2021). There are more than 5000 extant species of psocids, and they are present in a wide range of environments, including leaf litter, rotten wood, tree trunks and branches, bark, bird and mammal nests, rocks, caves, and domestic habitats. They are herbivorous and detritivorous, acting as nutrient recyclers of organic matter (New, 1987). Psocodea is divided into the suborders Trogiomorpha, Troctomorpha, and Psocomorpha (Smithers, 1972). The group Phthiraptera, which includes the parasitic lice, is considered an infraorder within Troctomorpha (de Moya et al., 2021). The Psocodea first appeared an estimated 375.7–292.4 Ma (Yoshizawa et al., 2019), supported by the oldest putative fossil barklouse from the Late Carboniferous (Nel et al., 2013). The psocids underwent diversification during the Cretaceous, with more than 70 described species belonging to the three suborders (Álvarez-Parra et al., 2020b, table 1). Furthermore, the extant genus *Psyllipsocus* is recorded from Cretaceous amber, showing the extraordinary evolutionary stasis or bradytely of this group of insects (Álvarez-Parra et al., 2020b; Jouault et al., 2021; Liang and Liu, 2021). Interestingly, the relative diversity of species in psocid suborders from the Cretaceous, albeit inferred from a fossil record biased towards resiniferous forests, is no longer reflected in present-day species (Álvarez-Parra et al., 2022). Nowadays

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Psocomorpha is the most diverse suborder of the group, but it is only represented in the Cretaceous by four species described so far (Vishniakova, 1975; Azar et al., 2015; Yoshizawa and Yamamoto, 2021).

The suborder Troctomorpha was divided into the infraorders Amphientometae and Nanopsocetae (Smithers, 1972). Nonetheless, de Moya et al. (2021) proposed a rearrangement of this suborder, increasing the number of infraorders to five: Amphientometae, Sphaeropsocetae, Pachytroctetae, Liposcelidetae, and Phthiraptera. Thus, the parasitic lice are better accommodated as an infraorder, and the former suborders of Phthiraptera are now considered parvorders (de Moya et al., 2021). Amphientometae includes the families Amphientomidae, Compsocidae, †Electrentomidae, Manicapsocidae, Musapsocidae, Troctopsocidae, and Protroctopsocidae; while Sphaeropsocetae, Pachytroctetae, and Liposcelidetae are monofamilial, respectively including Sphaeropsocidae, Pachytroctidae, and Liposcelididae. The suborder Psocomorpha contains 27 families within six infraorders (Yoshizawa and Johnson, 2014; Yoshizawa and Yamamoto, 2021): Archipsocetae, Caeciliusetae, Homilopsocidea, Philotarsetae, Epipsocetae, and Psocetae.

The fossil record of Psocodea in the Iberian Peninsula is poorly known and mainly represented by specimens in Cretaceous amber. To date, only six species within five genera have been described (Baz and Ortuño, 2000, 2001a,b; Álvarez-Parra et al., 2022). Furthermore, an only partial record assigned to cf. *Mesopsocus* sp. (Psocomorpha: Mesopsocidae) has been described from Spanish Miocene laminated mudstones (Peñalver et al., 1996). The study of the psocids in Spanish amber was revived by Álvarez-Parra et al. (2022), providing the descriptions of new Trogiomorpha specimens from five amber-bearing outcrops. Here, we present new troctomorphan species and a possible Psocomorpha morphotype from two amber-bearing outcrops of the Iberian Peninsula, and discuss their taxonomic placements and their palaeobiological implications.

2. Material and methods

The specimens studied in this work are included in amber pieces from two Cretaceous (Albian) amber-bearing outcrops in Spain: El Soplao (Cantabria Autonomous Community), also known as Rábago-El Soplao, and Ariño (Teruel Province). El Soplao is located in the north of the Iberian Peninsula, while Ariño is in the east (Fig. 1).

El Soplao outcrop is geologically located on the western margin of the Basque-Cantabrian Basin belonging to the Las Peñosas Formation (Najarro et al., 2009), which is dated as middle Albian based on foraminifera (García-Mondéjar, 1982). The amber-bearing level is related to a deltaic-estuarine palaeoenvironment (Najarro et al., 2009). Ariño amber is found in the bonebed level AR-1 within the Santa María open-pit coal mine located in the Maestrazgo Basin (Alcalá et al., 2012; Álvarez-Parra et al., 2021). The level AR-1 belongs to the Escucha Formation, and is dated as lower Albian based on the charophyte, ostracod, and palynological content (Tibert et al., 2013; Villanueva-Amadoz et al., 2015; Vajda et al., 2016; Álvarez-Parra et al., 2021). The Ariño amber palaeoenvironment is related to a freshwater swamp plain with shallow alkaline lakes and marine influence under a subtropical or tropical climate, inhabited by a highly diverse range of organisms (Alcalá et al., 2012; Álvarez-Parra et al., 2020a, 2021; Arillo et al., 2022).

Amber pieces were cut, polished, and embedded in epoxy resin prisms following the methodology of Corral et al. (1999), ensuring their preservation and protection. The amber pieces containing the studied specimens also include other syninclusions (e.g., the piece CES.057 has a total of seven syninclusions, and the piece CES.315 has a total of eight syninclusions). Therefore, thinner preparations are not possible as they would cause the loss of other specimens that might be studied in the future. Furthermore, the amber pieces from Ariño are usually turbid or containing particles hindering the visualisation of the bioinclusions, probably related to the palaeoenvironmental conditions of the resiniferous forest (Álvarez-Parra et al., 2021). The specimens were examined using an Olympus CX41 compound microscope with reflected and transmitted light. Photographs and drawings of the specimens were acquired using the same compound microscope with an attached sCMEX-20 digital camera and a camera lucida. The software ImageFocusAlpha version 1.3.7.12967.20180920 and Photoshop CS6 were used to take the photographs and prepare the figures, respectively. The anatomical nomenclature and systematics follow the works of Smithers (1972, 1990), Mockford (1993), and New and Lienhard (2007). Vein notation is as follows: Sc, Sc′, subcostal veins; Rs, R_1, R_{2+3}, R_{4+5}, radial veins; M, M_1, M_2, M_3, medial veins; Cu_1, Cu_2, cubital veins; A, 1A, 2A, anal veins.

This study includes five fossil psocid specimens. Their acronyms and provenances as well as the Spanish public institutions where they are housed are indicated below. The type locality of the new taxa is also indicated in the corresponding section of the systematic palaeontology.

Acronym CES: El Soplao amber. Housed in the Colección Institucional del Laboratorio de la Cueva El Soplao in Celis, Cantabria.

Acronym AR-1-A: Ariño amber. Housed in the Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis) in Teruel.

This manuscript has been registered in ZooBank under the number urn:lsid:zoobank.org:pub:C55EB54B-31F5-4C9B-93BF-48E34E309BAF.

3. Systematic palaeontology

Order **Psocodea** Hennig, 1966
Suborder **Troctomorpha** Roesler, 1940
Infraorder **Amphientometae** Pearman, 1936
Family Manicapsocidae Mockford, 1967

Genus ***Azarpsocus*** Maheu and Nel, 2020

Type species: *Azarpsocus perreaui* Maheu and Nel, 2020; by original designation and monotypy.

Original diagnosis (from Maheu and Nel, 2020). “Forewing: three-branched vein M, areola postica as long as high; vein A1 closely parallel to posterior wing margin; no crossvein between M and areola postica; A2 not fused with A1; pterostigma very long; hind wing: basal segment of Rs present; median vein simple.”

Remarks. Based on the new specimens here assigned to the genus *Azarpsocus*, the diagnosis is maintained as in the original except for one character that would be related to specific variability. Maheu and Nel (2020) indicated the same characters as being diagnostic for *Azarpsocus perreaui*, adding ‘maxillary palp 2 (mx2) as long as maxillary palp 4 (mx4)’. We consider that ‘areola postica as long as high’ should be included in the specific diagnosis of *A. perreaui* and excluded from that of the genus *Azarpsocus*.

Azarpsocus anjana Álvarez-Parra and Nel, sp. nov.
Figs. 2–4

This new species has been registered in ZooBank under the number urn:lsid:zoobank.org:act:D7707F15-79FB-422F-9A49-F535734E98DF.

Type material. Holotype CES.057.3; a complete specimen (Fig. 2), sex unknown; syninclusion with one arachnid, two beetles, and three

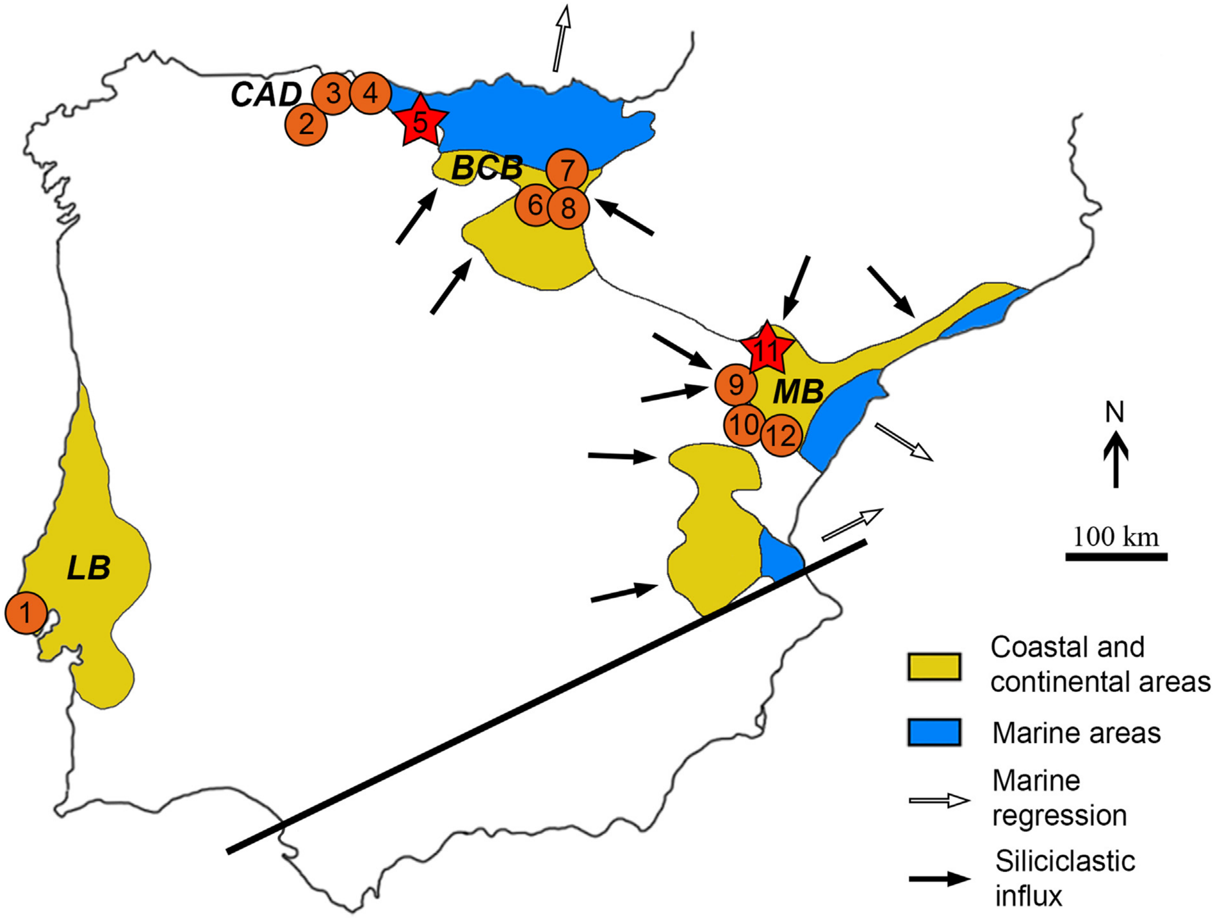

Fig. 1. Map of the Iberian Peninsula showing sedimentary basins during the early–middle Albian and indicating the location of the 12 amber-bearing outcrops with bioinclusions reported in Spain and Portugal to date: Lusitanian Basin (LB), Central Asturian Depression (CAD), Basque-Cantabrian Basin (BCB), and Maestrazgo Basin (MB). Provenances of studied specimens indicated with red stars. 1) Estoril-Cascais, 2) El Caleyu, 3) La Rodada, 4) Pola de Siero, 5) El Soplao or Rábago-El Soplao, 6) Salinillas de Buradón, 7) Peñacerrada I, 8) Peñacerrada II, 9) San Just, 10) Arroyo de la Pascueta, 11) Ariño, 12) La Hoya. Map modified from Mas et al. (2004).

hymenopterans. Housed in the Colección Institucional del Laboratorio de la Cueva El Soplao in Celis, Rábago, Cantabria.

Other material. AR-1-A-2019.58.1; a partial specimen (Fig. 3C, D), sex unknown; syninclusion with a hymenopteran. AR-1-A-2019.60.1, a partial specimen (Fig. 3A, B), sex unknown; syninclusion with a beetle and a dipteran.

Locality and horizon. El Soplao amber-bearing outcrop, Cantabria Autonomous Community, Spain; Las Peñosas Formation, middle Albian, Lower Cretaceous (Najarro et al., 2009).

Other localities. Ariño amber-bearing outcrop, Teruel Province, Spain; Escucha Formation, lower Albian (Álvarez-Parra et al., 2021).

Etymology. After Anjana, a benevolent fairy in Cantabrian mythology.

Diagnosis. Forewing with R_1 strongly curved at its distal part forming a long and bulging pterostigma, areola postica 2× longer than wide, Cu_{1a} strongly curved, forming a bulging areola postica.

Description. Body length of the holotype CES.057.3 from clypeus to distal part of abdomen is 0.97 mm (Fig. 2A, B). No setae on body surface. Head 0.34 mm wide; epicranial suture and ocelli not visible; small and bulging compound eyes 0.06 mm in diameter; number of ommatidia indiscernible; antenna with 13 flagellomeres covered by setae; first flagellomere long and slightly curved; length of flagellomeres: I 0.18 mm, II 0.15 mm, III 0.14 mm, IV 0.10 mm, V 0.10 mm, VI 0.08 mm, VII 0.08 mm, VIII 0.08 mm, IX 0.06 mm, X 0.04 mm, XI 0.04 mm, XII 0.04 mm, XIII 0.4 mm; secondary annulations uncertain; bulging clypeus; mouthparts obscure, only left distal maxillary palpomere and probably lacinia visible. Thorax 0.35 mm long. Forewing completely preserved in the holotype CES.057.3 (Fig. 2C) and in AR-1-A-2019.60.1 (Fig. 3A, B), partially preserved in AR-1-A-2019.58.1 (Fig. 3C, D); length and maximum width (in mm) of forewing 1.92:0.73 (holotype CES.057.3), 2.84:1.06 (AR-1-A-2019.60.1); membrane hyaline; margin and membrane glabrous; basal section of Sc short and curved, joining R; distal section of Sc short and slightly curved; R_1 strongly curved at its distal part, forming a long and bulging pterostigma; pterostigma not coloured; pterostigma of AR-1-A-2019.60.1 apparently with an area close to costal margin more marked than rest of the membrane probably due to taphonomic artefact; highly sclerotised point emerging of distal of Sc in AR-1-A-2019.58.1; basal section of Rs straight in the holotype CES.057.3, while curved in the other specimens; Rs and M fused for a short distance; Rs bifurcating into R_{2+3} and R_{4+5} nearly at level of R_1 reaching margin; M three-branched; bifurcation of M_1 and M_2 slightly distal to bifurcation of Rs; emerging of M_3 slightly basal to bifurcation of Rs; areola postica free, 2× longer than wide; Cu_{1a} strongly curved, forming a bulging areola postica; Cu_{1b} short; Cu_2 and A joining in a nodulus close to margin; A parallel to posterior margin; second anal vein not visible in any specimen. Hind wing completely preserved in the holotype CES.057.3 (Fig. 3D), partly preserved in AR-1-A-2019.58.1 (Fig. 3C, D) and AR-1-A-2019.60.1 (Fig. 3A, B); length and maximum width (in mm) of hind wing 1.46:0.49 (holotype CES.057.3), 2.45:0.74 (AR-1-A-2019.60.1); membrane hyaline; margin and

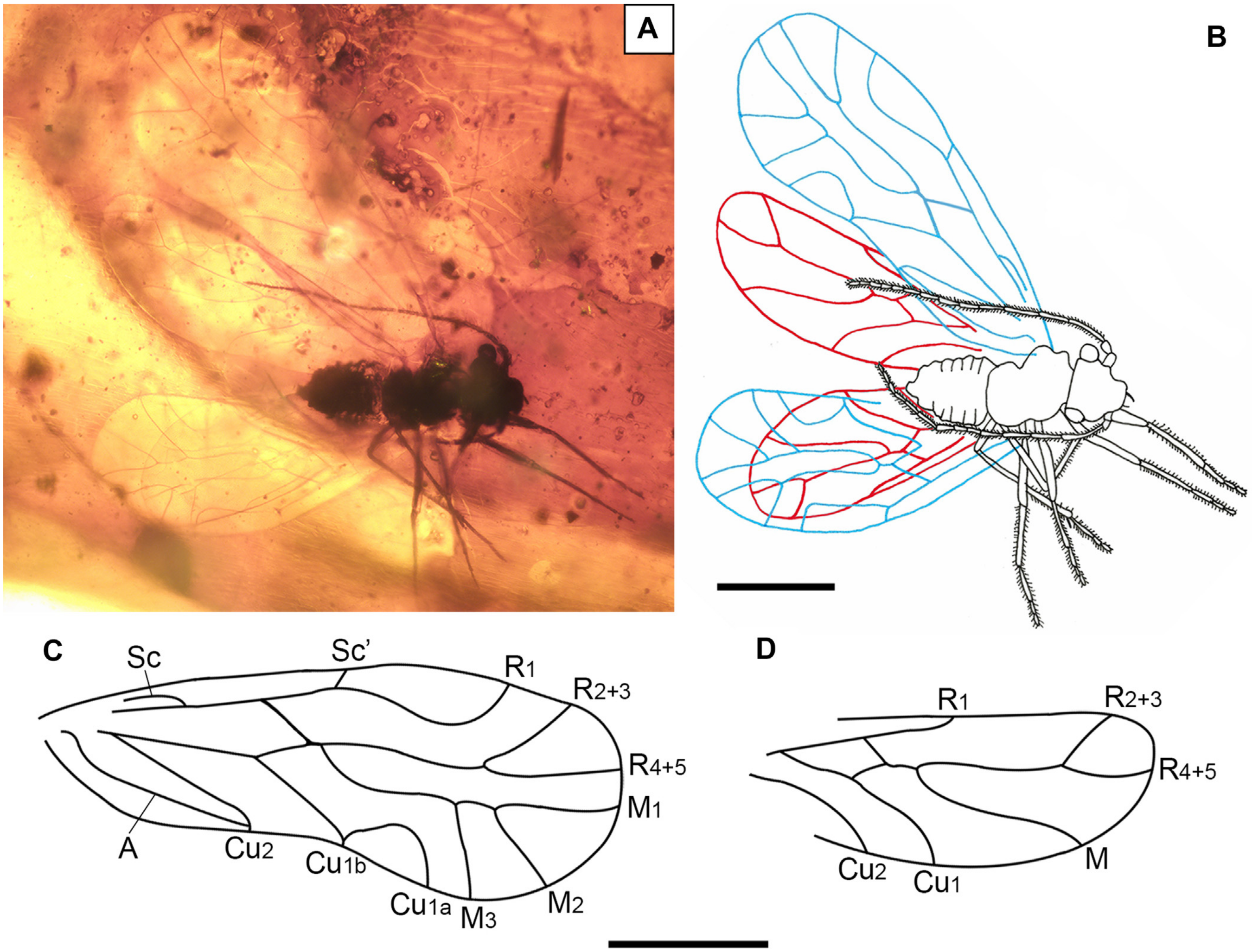

Fig. 2. *Azarpsocus anjana* Álvarez-Parra and Nel sp. nov. (Psocodea: Troctomorpha: Manicapsocidae), holotype CES.057.3, sex unknown, middle Albian amber from El Soplao (Cantabria Autonomous Community, Spain): A, B) photograph and drawing of the specimen in dorsal view, forewings in blue and hind wings in red, both at same scale; C, D) forewing and hind wing, respectively, both at same scale. Scale bars = 0.5 mm.

membrane glabrous; Sc not visible; R_1 reaching margin closer to base of Rs in the holotype CES.057.3 and AR-1-A-2019.58.1 than in AR-1-A-2019.60.1; Rs and M fused for a short distance; Rs two-branched; M unbranched; Cu_1 and Cu_2 present; bifurcation of anal vein near margin visible in AR-1-A-2019.60.1. Legs covered by setae; one distal spur on tibiae visible in the holotype CES.057.3 and in AR-1-A-2019.58.1; three tarsomeres; proximal tarsomere the longest; pulvillus and preapical tooth unclear in the specimens. Abdomen obscure; five segments can be observed in the holotype CES.057.3; genitalia not visible in any specimen.

Discussion. The holotype specimen CES.057.3 fits within the family Manicapsocidae based on the characters: body and wings without scales, 15 antennomeres (13 flagellomeres), macropterous, forewing venation not reduced, pterostigma not coloured and closed basally (distal section of Sc present), nodulus present, hind wing with M unbranched, and tarsi three-segmented (Mockford, 1967; Smithers, 1972, 1990). Key characters, such as presence of second anal vein in forewings and one preapical tooth on pretarsal claws, as well as characters of the genitalia, are challenging to observe in fossil specimens that are not exceptionally well-preserved. Considering the genera within Manicapsocidae, the holotype CES.057.3 shows a similar venation to *Azarpsocus perreaui* from Burmese amber (Fig. 4). Furthermore, most of the diagnostic characters of the genus (Maheu and Nel, 2020) are present in CES.057.3, such as forewing with very long pterostigma, M three-branched, vein 1A closely parallel to posterior wing margin, no crossvein between M and areola postica, and hind wing with basal segment of Rs present and M simple. The only diagnostic characters of the genus absent in CES.057.3 are 'second anal not fused with first anal vein' (second anal vein not visible) and 'areola postica as long as high'. We propose to move the latter to the diagnostic characters of the species *A. perreaui* (see above). The main differences between CES.057.3 and *A. perreaui* concern the shape of the pterostigma and the areola postica. Therefore, we consider that these data support the description of a new species, *Azarpsocus anjana* sp. nov., closely related to *A. perreaui*. Unfortunately, the secondary annulations described in *A. perreaui* cannot be observed in the holotype of the new species. The other two studied specimens, not in the type series, show the same wing venation as the holotype, thus we believe that the most parsimonious way is to consider them conspecific. Nonetheless, these specimens are poorly preserved and few body characters are visible; furthermore, some parts of the wings cannot be observed either. Therefore, new findings in the future might prove or refute our statement in

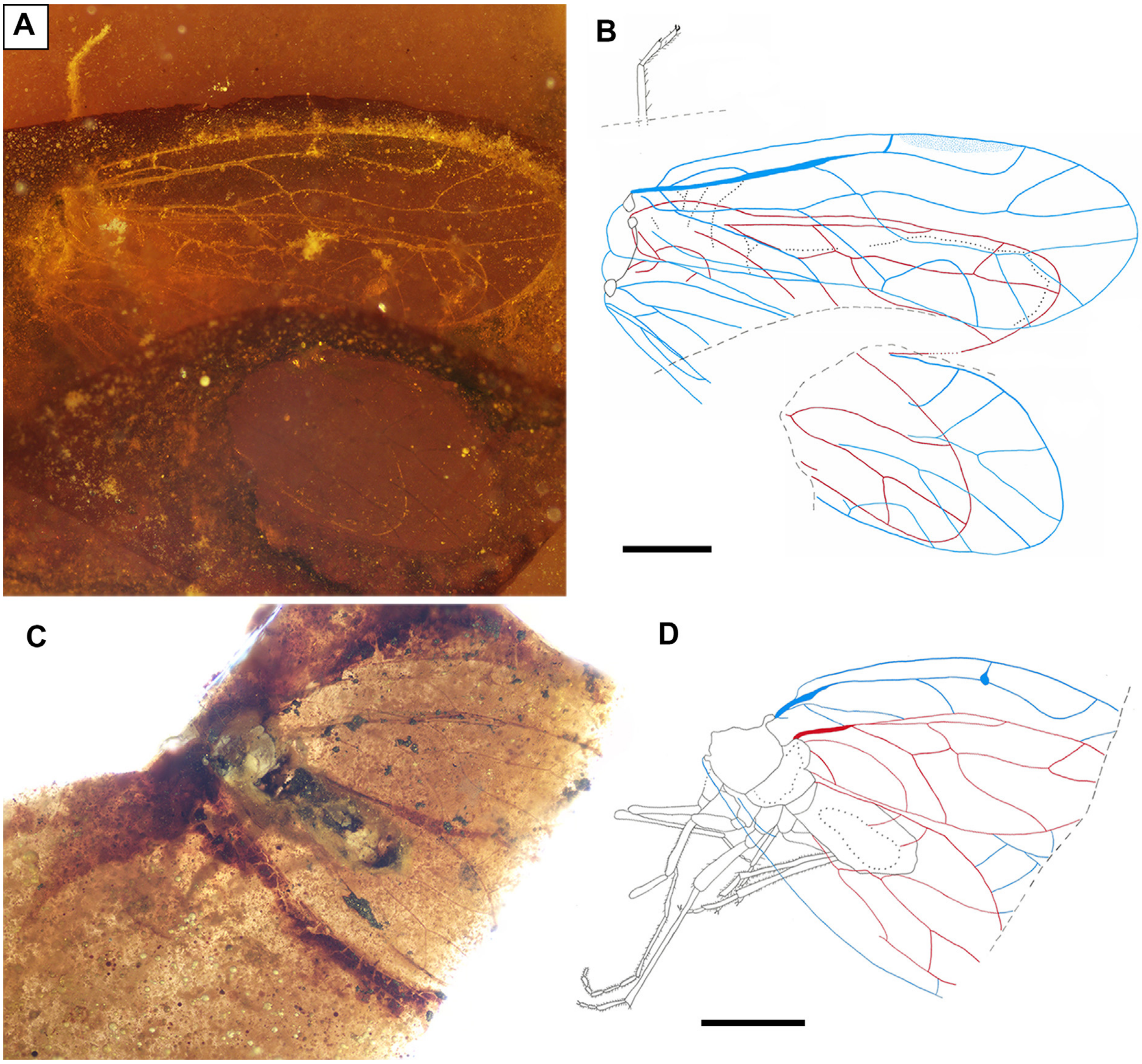

Fig. 3. *Azarpsocus anjana* Álvarez-Parra and Nel sp. nov. (Psocodea: Troctomorpha: Manicapsocidae), lower Albian amber from Ariño (Teruel Province, Spain): A, B) photograph and drawing of the habitus of AR-1-A-2019.60.1 in dorsal view, sex unknown, forewings in blue and hind wings in red, both at same scale; C, D) photograph and drawing of the habitus of AR-1-A-2019.58.1 in dorsal view, sex unknown, forewings in blue and hind wings in red, both at same scale. Scale bars = 0.5 mm.

relation to its taxonomic placement. It is interesting to note the difference in size of all these specimens, the holotype being the smallest, similar in size to the holotype of *A. perreaui* (Maheu and Nel, 2020). Furthermore, in the holotype and AR-1-A-2019.58.1, R_1 in hind wing reaches the wing margin closer to base of Rs than in AR-1-A-2019.60.1. These differences might be explained by intraspecific variability and teratism.

The genus *Azarpsocus* shows a venation similar to the *Caecilius*-type present in several groups within Psocomorpha (Smithers, 1972); most notably, it is strikingly similar to that of the family Lachesillidae (infraorder Homilopsocidea). Furthermore, they share glabrous wings and the presence of a preapical tooth on pretarsal claws (Smithers, 1972). The placement of the genus *Azarpsocus* within Lachesillidae is ruled out based on several characters (Smithers, 1972, 1990; Mockford, 1993; New and Lienhard, 2007): 15 antennomeres (psocomorphans have 13 or fewer), flagellomeres secondarily annulated at least in the species *Azarpsocus perreaui* (not secondarily annulated in psocomorphans), ocelli not grouped in a tubercle (ocelli in a tubercle is typical of homilopsocideans), pterostigma not coloured (usually coloured in psocomorphans), short basal section of Sc joining R in forewing (character typical of manicapsocids), hind wing with Rs fused with M for a short distance (fused for a relatively long distance in lachesillids), and three-segmented tarsi (two-segmented in lachesillids). Nonetheless, the coloured pterostigma might be a character depending on intraspecific variability; in addition, the lachesillid *Eolachesilla chilensis* Badonnel, 1967 shows three-segmented tarsi (New and Lienhard, 2007). Therefore, we prefer to maintain the bispecific genus *Azarpsocus* as belonging to Manicapsocidae. It is possible that new psocid specimens with *Caecilius*-type venation will be described from Cretaceous amber, thus helping to discern the anatomical differences between manicapsocids and psocomorphans. The genus *Azarpsocus* shows a wing venation clearly different to other Cretaceous barklice genera, only sharing characteristics with the genus *Paramesopcus*, although it has two-branched medial vein in hind wing (Azar et al., 2008; Maheu and Nel, 2020).

Azarpsocus anjana sp. nov. is present in El Soplao (middle Albian) and Ariño (early Albian) ambers. These findings might suggest morphological stasis for this species in Iberia throughout the

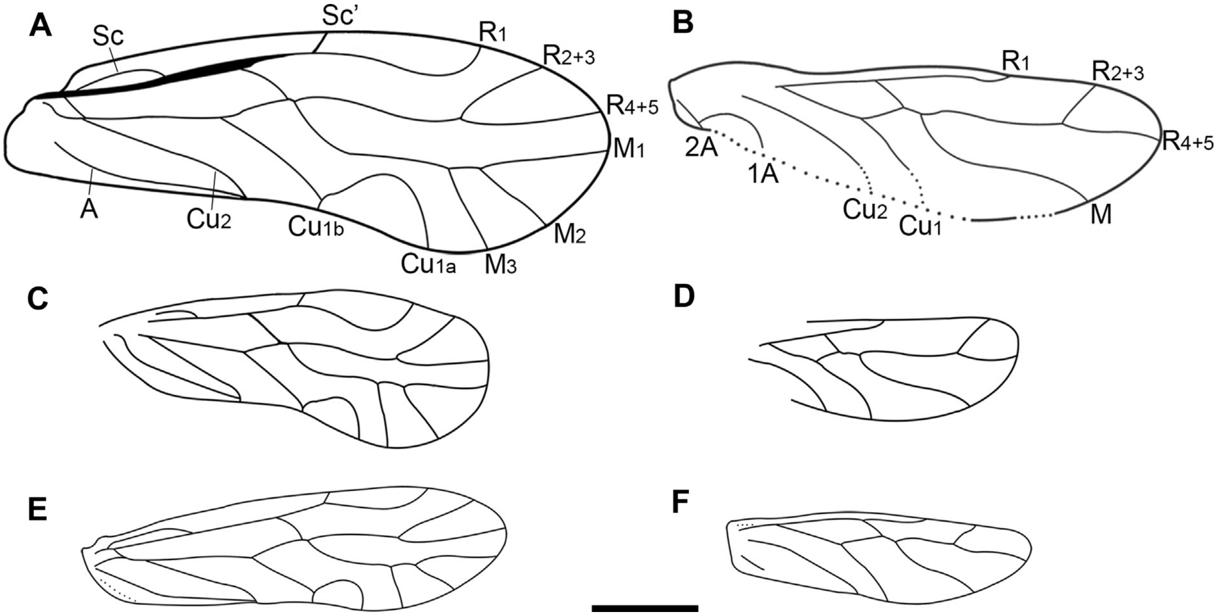

Fig. 4. Comparison of wing morphotypes and sizes in *Azarpsocus* (Psocodea: Troctomorpha: Manicapsocidae): A, B) forewing and hind wing of *Azarpsocus anjana* Álvarez-Parra and Nel sp. nov. specimen AR-1-A-2019.60.1 (Ariño, lower Albian); C, D) forewing and hind wing of *Azarpsocus anjana* sp. nov. holotype CES.057.3 (El Soplao, middle Albian); E, F) forewing and hind wing of *Azarpsocus perreaui* (Burmese amber, Myanmar, lower Cenomanian), interpreted from photograph in Maheu and Nel (2020). All at same scale. Scale bar = 0.5 mm.

Albian, despite minor differences in size and some characters related to usual teratism in barklice, such as the length of R_1 in hind wings.

Superfamily **Electrentomoidea** Enderlein, 1911
Family Compsocidae Mockford, 1967
Genus ***Burmacompsocus*** Nel and Waller, 2007

Type species: *Burmacompsocus perreaui* Nel and Waller, 2007; by original designation and monotypy.
Other species: *Burmacompsocus banksi* (Cockerell, 1916), *B. coniugans* Sroka and Nel, 2017, and *B. pouilloni* Ngô-Muller, Garrouste and Nel, 2020.

Burmacompsocus ojancano Álvarez-Parra and Nel, sp. nov.
Fig. 5

This new species has been registered in ZooBank under the number urn:lsid:zoobank.org:act:17523BC3-06C7-41D7-98B5-9508BCCABEB2.
Type material. Holotype CES.315.8; incomplete macropterous specimen with poorly preserved body but nearly complete venation preserved (Fig. 5A, B), sex unknown; syninclusion with one beetle, two hymenopterans, and four dipterans. Housed in the Colección Institucional del Laboratorio de la Cueva El Soplao in Celis, Rábago, Cantabria.
Locality and horizon. El Soplao amber-bearing outcrop, Cantabria Autonomous Community, Spain; Las Peñosas Formation, middle Albian, Lower Cretaceous (Najarro et al., 2009).
Etymology. After Ojáncano, an evil one-eyed giant in Cantabrian mythology.
Diagnosis. Forewing with short basal section of Sc, Rs contacting M in a point, bulging areola postica with Cu_{1a} strongly curved, areola postica 1.5× longer than pterostigma; hind wing with Sc long fused to R_1, Cu_1 strongly curved before reaching margin.
Description. No flattened scales on body or wings. One antenna partly preserved, with at least nine visible flagellomeres; length of the basal flagellomeres around 0.08 mm; length of the distal flagellomeres around 0.04 mm; secondary annulations absent on flagellomeres. Forewing 1.90 mm long and 0.80 mm maximum width (Fig. 5C); membrane hyaline; margin and membrane glabrous; microvestiture on forewing membrane in form of microtrichia; basal section of Sc short and strongly curved, joining R at 0.44 mm from wing base; closed pterostigma 0.26 mm long and 0.08 mm wide, not coloured, formed by a short distal section of Sc reaching margin at 1.21 mm from wing base, and slightly curved R_1 reaching margin at 1.40 mm from wing base; Rs showing a single point of contact with M, neither fused; no crossvein between R_1 and Rs; bifurcation of Rs into R_{2+3} and R_{4+5} at 1.20 mm from wing base; both veins long, slightly curved and reaching margin at 1.70 mm and 1.81 mm from wing base, respectively; M three-branched; M_3 emerging at 1.36 mm from wing base, running almost straight to margin, joining at 1.64 mm from wing base; bifurcation of M_1 and M_2 not visible; both veins nearly straight; M_1 reaching wing apex; M_2 reaching wing margin at 1.80 mm from wing base; areola postica 0.39 mm long and 0.17 mm wide; crossvein between M and areola postica absent; Cu_{1a} bulging and strongly curved, reaching wing margin at 1.43 mm from wing base; Cu_{1b} short and reaching wing margin at 1.04 mm from wing base; Cu_2 and A veins present, joining in a nodulus. Hind wing 1.56 mm long and 0.55 mm wide (Fig. 5D); membrane hyaline; margin and membrane glabrous; Sc long fused to R_1, emerging at 0.59 mm from wing base; R_1 slightly curved; basal section of Rs absent; Rs two-branched and bifurcating into R_{2+3} and R_{4+5} at 1.11 mm from wing base; M two-branched and bifurcating into M_1 and M_2 at 0.98 mm from wing base; Cu_1 and Cu_2 present; Cu_1 with a strong curve before reaching margin. Legs partly preserved; two distal spurs on hind tibia; right hind tibia 0.74 mm long; right hind tarsus 0.43 mm long; three-segmented tarsi; length of tarsomeres of right hind leg: proximal 0.29 mm, middle 0.07 mm, distal 0.07 mm; pretarsal claws not visible. Abdomen partly preserved; characters of genitalia cannot be described.
Discussion. The holotype specimen CES.315.8 belongs to the family Compsocidae, within Amphientometae (Troctomorpha), based on body and wings without flattened scales, macropterous wings, not

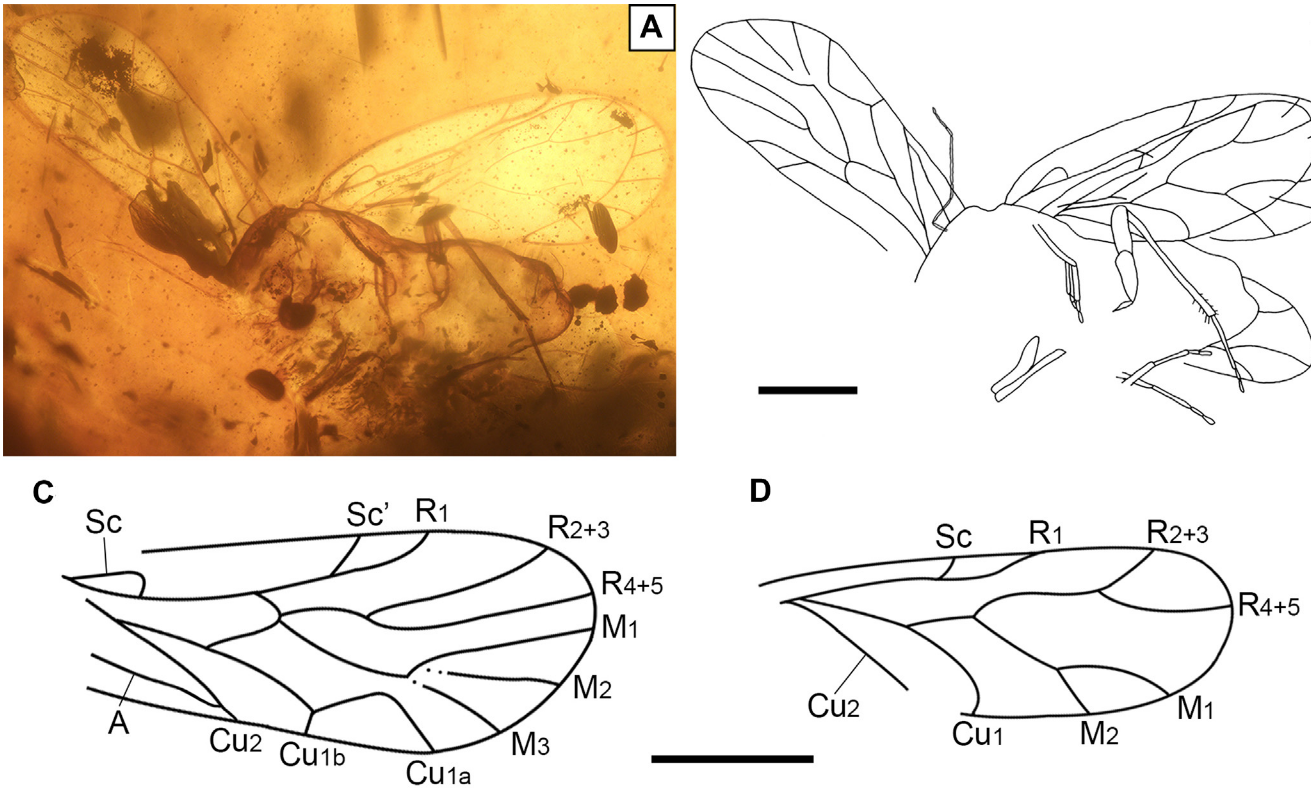

Fig. 5. *Burmacompsocus ojancano* Álvarez-Parra and Nel sp. nov. (Psocodea: Troctomorpha: Compsocidae), holotype CES.315.8, sex unknown, middle Albian amber from El Soplao (Cantabria Autonomous Community, Spain): A, B) photograph and drawing, both at same scale; C, D) forewing and hind wing, both at same scale. Scale bars = 0.5 mm.

reduced forewing venation, pterostigma that is closed basally and not coloured, hind wing with M two-branched, and three-segmented tarsi (Smithers, 1972; Nel and Waller, 2007). Interestingly, Mockford (1967) and Smithers (1972) indicated hind wing with unbranched M, even though the drawings in Banks (1930, plate 9: figure 4) and Mockford (1967) clearly show M two-branched in the type genus *Compsocus* and in *Electrentomopsis*. The presence of a nodulus is a key character of the family (Nel and Waller, 2007). Members of Compsocidae show forewings with two anal veins, 2A joining 1A, and two preapical teeth on pretarsal claws (Mockford, 1967). The specimen CES.315.8 only shows one anal vein and pretarsal claws are not visible, both probably due to preservation artefact. Within Compsocidae, CES.315.8 falls in the genus *Burmacompsocus* based on venation similar to the previously described species (Nel and Waller, 2007; Sroka and Nel, 2017; Ngô-Muller et al., 2020): forewing with basal section of Sc short and joining R, triangular pterostigma shape, short basal section of Rs, short M_{1+2}, M_3 separating distal to bifurcation of R_{2+3} and R_{4+5} and nearly aligned with M, long areola postica, nodulus separated by a short distance from wing margin, hind wing with basal section of Rs absent, Rs curved and two-branched, M straight and two-branched, and separation of R_{2+3} and R_{4+5} distal to separation of M_1 and M_2. The diagnosis of *Burmacompsocus* includes forewing with microvestiture in the form of microtrichia and hind wing without basal section of Rs (Nel and Waller, 2007), as in CES.315.8. The shape of the areola postica, its proportional length in relation to the pterostigma, and hind wing with Sc long fused to R_1, and strongly curved Cu_1, as observed in CES.315.8, are unique characters within the genus, supporting the description of *Burmacompsocus ojancano* sp. nov. The basal section of Sc in forewings is longer in *B. perreaui* and *B. pouilloni* than in the new species; furthermore, Sc is briefly fused to R_1 in hind wings of *B. perreaui* and *B. pouilloni* (Nel and Waller, 2007; Ngô-Muller et al., 2020). *Burmacompsocus ojancano* sp. nov. differs from *B. coniugans* in the Rs showing a single point of contact with M in forewings (vs. briefly fused) (Sroka and Nel, 2017). *Burmacompsocus banksi* was included in the genus *Psyllipsocus* by Cockerell (1916), but later transferred to the genus *Burmacompsocus* by Mockford et al. (2013), who noted the similarity with *B. perreaui*. Interestingly, the representatives of the species within *Burmacompsocus* show M_3 nearly aligned with M in forewings, except for *B. coniugans*. The Cretaceous species *Paraelectrentomopsis chenyangcaii* has a crossvein between Rs and M, and M bifurcates into M_1 and M_2+M_3 (Azar et al., 2016); these two characters differ from *B. ojancano* sp. nov. The family Compsocidae comprises only two extant species (Mockford, 1967): *Compsocus elegans* Mockford, 1967 and *Electrentomopsis variegatus* Mockford, 1967. The character 'basal section of Rs in hind wing' is present in *C. elegans*, but not in *E. variegatus* (Mockford, 1967). Anal veins 1A and 2A join in *E. variegatus*, differing from *Burmacompsocus* (Nel and Waller, 2007). The description of new complete specimens with the same venation morphotype may support the erection of a new genus within Compsocidae. Notably, the extant species of the family are only found in Central America, whereas the fossil representatives come from Cretaceous deposits in Spain and Myanmar, indicating an ancient wide distribution of the group. The living species would correspond to a relict fauna.

The members of Manicapsocidae and Compsocidae show similarities and are probably phylogenetically closely related (Mockford, 1967), diverging during the Early Cretaceous (Baz and Ortuño, 2001a). Interestingly, the wing venation of *Manicapsocidus enigmaticus* is strikingly similar to that of

Burmacompsocus ojancano sp. nov., sharing the shape of the pterostigma and the areola postica, but differing in the presence of vein rs-m and the arrangement of M branches in *M. enigmaticus* forewing. Furthermore, the hind wing of the new species shows Sc emerging from R_1 and M is two-branched (vs. Sc absent and M unbranched).

Description of a possible Psocomorpha morphotype

Morphotype Ariño

Figs. 6, 7

Material. AR-1-A-2019.50.3; partial macropterous specimen, sex unknown; syninclusion with two dipterans. Housed in the Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis).

Locality and horizon. Ariño amber-bearing outcrop, Teruel Province, Spain; Escucha Formation, lower Albian, Lower Cretaceous (Álvarez-Parra et al., 2021).

Description. Body length from frontal part of clypeus to distal part of abdomen, 1.44 mm (Fig. 6A, B). Setae not visible on body surface. Head 0.39 mm wide; no ocelli visible; bulging compound eyes, some ommatidia visible in right eye; bulging clypeus; antennae spectrally preserved with the total number of flagellomeres difficult to discern; scape, pedicel, and some flagellomeres visible, apparently covered by a few setae; first and second flagellomeres apparently longer than rest; secondary annulations cannot be observed; mouthparts not visible. Thorax preserved as a hollow structure. Right wings preserved. Forewing 1.67 mm long and 0.62 mm maximum width (Fig. 7A, C); membrane hyaline; margin and membrane glabrous; membrane with microtrichia; costal margin partly thickened; basal section of Sc poorly visible, but it seems to end in the membrane, not joining R or margin; pterostigma long and flat, with distal part somewhat bulging, 0.45 mm long and 0.08 mm maximum width; short distal section of Sc arising from a highly sclerotised point of R, reaching margin at 0.91 mm from wing base; R_1 reaching margin at 1.34 mm from wing base; Rs only showing a single point of contact with M, these are not fused and there is no crossvein between the two veins; Rs bifurcating into R_{2+3} and R_{4+5} at 1.23 mm from wing base; R_{2+3} and R_{4+5} slightly curved, reaching margin at 1.56 mm and 1.63 mm from wing base, respectively; M two-branched, bifurcating into M_1 and M_2 at 1.29 mm from wing base, slightly distal to bifurcation of Rs; M_1 reaching margin at 1.63 mm from wing base; M_2 reaching margin at 1.46 mm from wing base; area between branches of M 1.5× wider than that between branches of Rs (at maximum width of both areas); Cu emerging from M + Cu at nearly the same level as

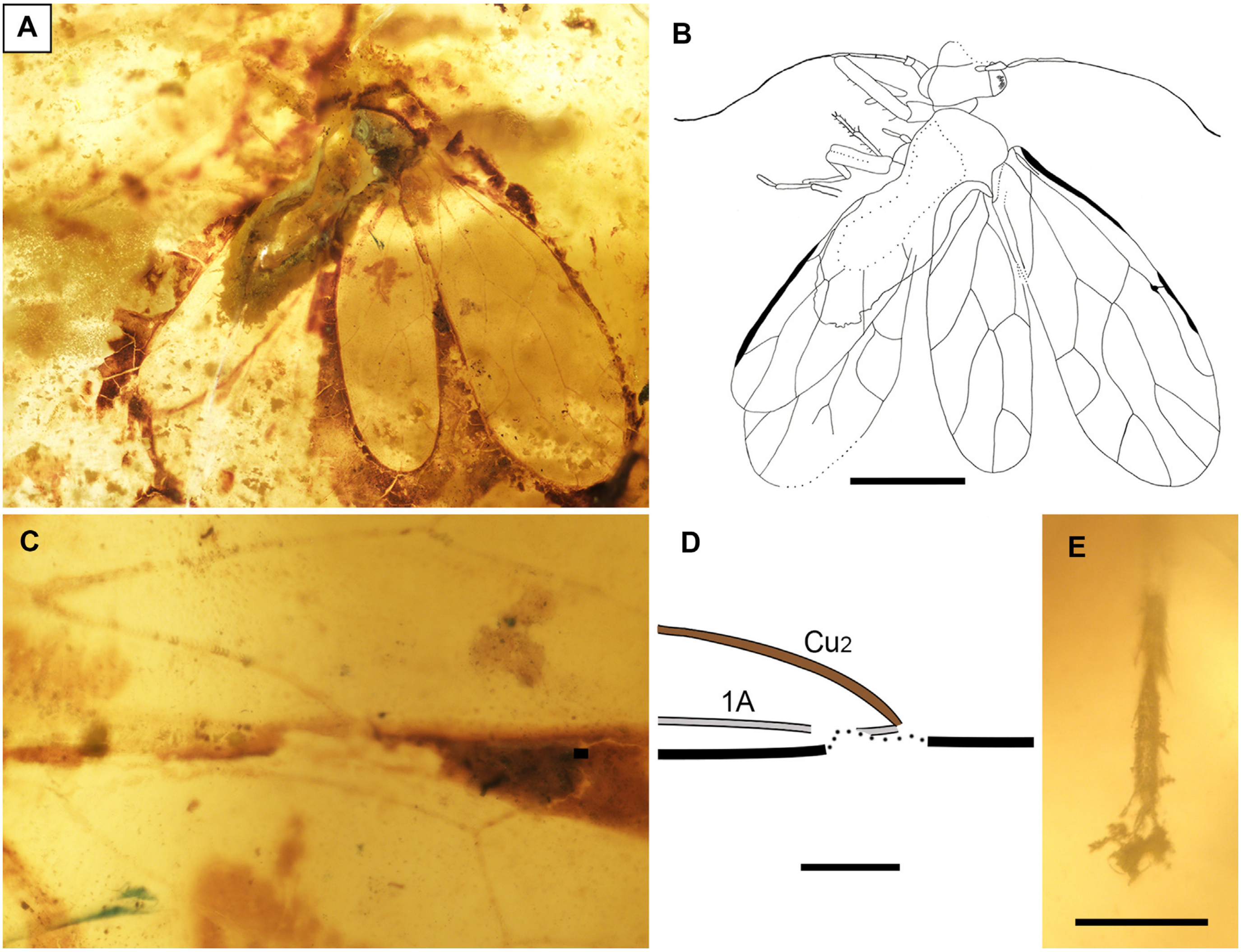

Fig. 6. Morphotype Ariño (Psocodea: Psocomorpha?), AR-1-A-2019.50.3, sex unknown, early Albian amber from Ariño (Teruel Province, Spain): A, B) photograph and drawing of the habitus in dorsal view, both at same scale; C, D) photograph and drawing of nodulus of right forewing, both at same scale; E) distal part of tarsus of mid leg. Scale bars = 0.5 mm (A, B), 0.1 mm (C–E).

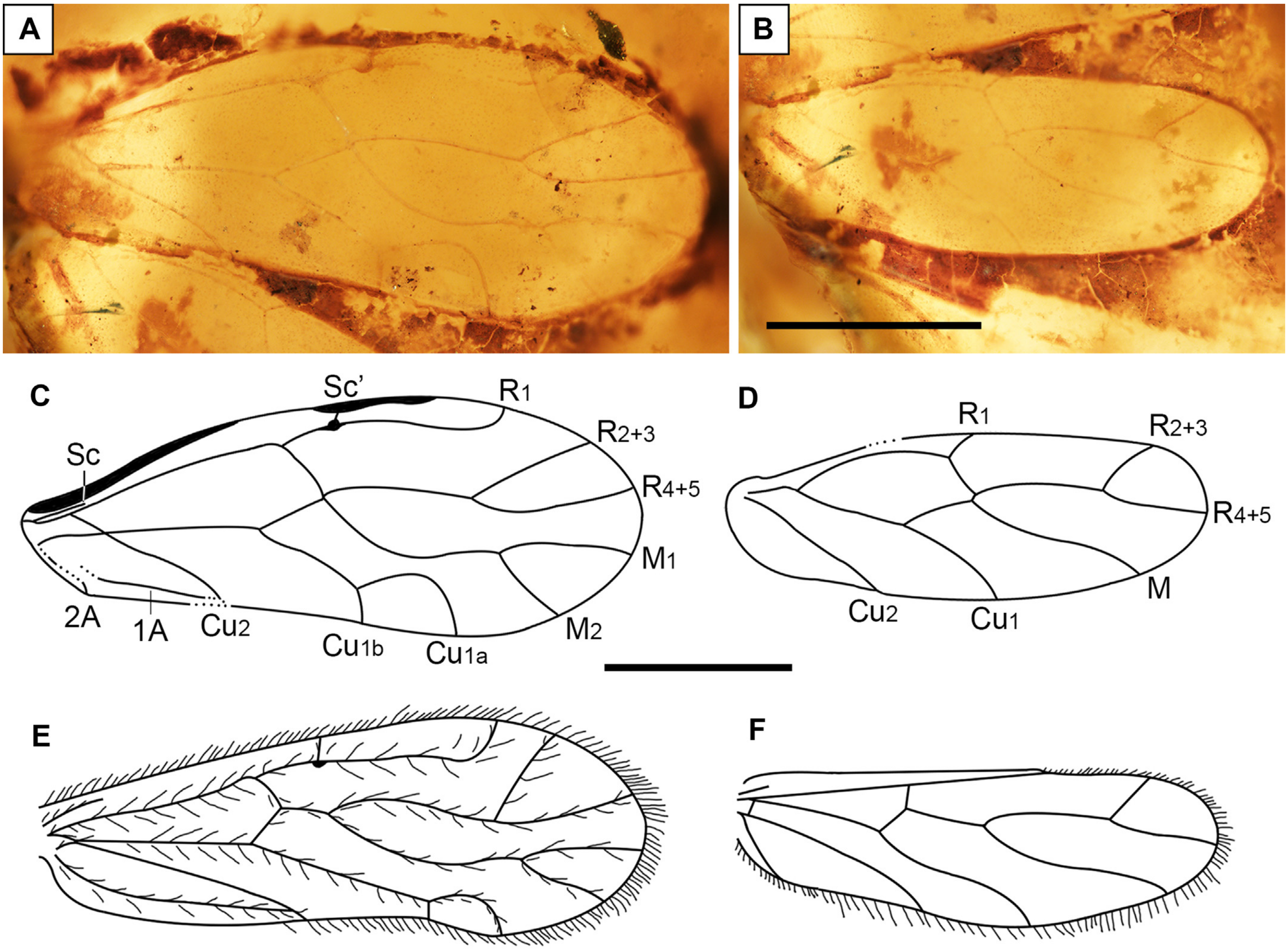

Fig. 7. Wings of morphotype Ariño (Psocodea: Psocomorpha?), specimen AR-1-A-2019.50.3, and *Scottiella micans* Enderlein, 1931 (Psocodea: Psocomorpha: Pseudocaeciliidae) for comparison: A, B) photograph of forewing and hind wing of morphotype Ariño, respectively, both at same scale; C, D) drawing of forewing and hind wing of morphotype Ariño, respectively; E, F) forewing and hind wing of female *S. micans*, respectively, redrawn from Enderlein (1931). C–F at same scale. Scale bars = 0.5 mm.

Rs emerges from R; areola postica short and bulging, 0.25 mm long and 0.15 mm wide; strongly curved Cu$_{1a}$ reaching margin at 1.23 mm from wing base; straight Cu$_{1b}$ reaching margin at 0.96 mm from wing base; Cu$_{1b}$ 2.5× longer than shortest distance between M and Cu$_{1a}$; Cu2 and 1A joining in a nodulus at 0.59 mm from wing base (Fig. 6C, D); 2A partly visible, joining margin near wing base. Hind wing 1.27 mm long and 0.43 mm maximum width (Fig. 7B, D); membrane hyaline; margin and membrane glabrous; membrane with microtrichia; Sc not visible; curved R; short and straight R$_1$ reaching margin at 0.64 mm from wing base; crossvein rs-m 0.03 mm long; Rs two-branched, bifurcating at 0.97 mm from wing base; R$_{4+5}$ reaching margin at wing apex; M unbranched; five-angled basi-radial cell; Cu$_1$ and Cu$_2$ present; anal veins not visible. Legs partly visible; thin femora and tibiae; tarsi seem to be two-segmented (Fig. 6E), covered by setae; proximal tarsomere of hind leg 0.18 mm long; distal tarsomere of mid leg 0.10 mm long; one distal spur on proximal tarsomere; pretarsal claws without preapical tooth or pulvillus (Fig. 6E). Abdomen incomplete and observation hindered by left wings; genitalia cannot be described.

Discussion. The specimen AR-1-A-2019.50.3 shows a peculiar venation in forewing and hind wing that is not known from other Cretaceous psocids. Nonetheless, due to poor preservation, it lacks key characters required to obtain an accurate identification, such as the number of flagellomeres (and the presence or absence of secondary annulations on them). Regarding the families within Trogiomorpha and Troctomorpha, the studied specimen is only similar to the Pachytroctidae, based on forewing with M two-branched and hind wing with unbranched M (Smithers, 1972). It also shares these characters with the genus *Palaeomanicapsocus* (Manicapsocidae) from Cenomanian Burmese amber (Azar et al., 2017), and with *Libanopsyllipsocus alexanderasnitsyni* Azar and Nel, 2011 from Barremian Lebanese amber, assigned to the family Psyllipsocidae by Azar and Nel (2011), but belonging to Pachytroctidae *sensu* Mockford et al. (2013). The specimen differs from all of them in the shape of the pterostigma and the areola postica. Furthermore, the family Pachytroctidae lacks a nodulus (Smithers, 1972; Mockford, 1993). The presence of a nodulus in forewing and the two-segmented tarsi links the studied specimen to the suborder Psocomorpha (Smithers, 1972; Mockford, 1993). Within Psocomorpha, the wing venation of the studied specimen is strikingly similar to that of the genera *Mepleres* Enderlein, 1926 and *Scottiella* Enderlein, 1931 (Fig. 7E, F) (Enderlein, 1926, 1931; Smithers, 1972; New and Lienhard, 2007), which both belong to the family Pseudocaeciliidae (infraorder Philotarsetae).

The genus *Mepleres* comprises more than 60 species distributed in Jamaica, Africa, South-East Asia, and Oceania (New and Lienhard, 2007). The genus *Scottiella* includes three species from Seychelles

(Enderlein, 1931). Currently, they are the only two genera of pseudocaeciliids showing a M two-branched on the forewing, following the synonymy of *Pseudoscottiella* and *Meniscopsocus* under *Mepleres* (Yoshizawa, 2000). The most important difference between these two genera and the studied specimen is the presence of setae on the forewing margin and veins and on the margin of the hind wing (Enderlein, 1931; New and Lienhard, 2007), while the wings of the specimen from Ariño are completely glabrous. Other minor forewing differences are the Rs and M fused for a length (vs. showing a single point of contact in the studied specimen) and the absence of a second anal vein (vs. partly visible). The hind wings of *Mepleres* and *Scottiella* show a long R_1 until reaching the margin (vs. short in the studied specimen), Rs and M fused for a length (vs. not fused and presence of a crossvein rs-m); the presence of Sc and an anal vein in these wings are characters that are not visible in the specimen. The two genera and the specimen from Ariño share the absence of a preapical tooth in pretarsal claws. The differences between the studied specimen and these genera prevent its inclusion within any of them, while the lack of setae on wings and Rs and M not fused in forewing or hind wing rule out its membership of the Pseudocaeciliidae and Philotarsetae (Smithers, 1972).

The vein 2A in forewing, partly visible in the studied specimen, is present in Epipsocetae within Psocomorpha as a secondary derived character (Casasola González, 2006). The studied specimen apparently does not fit in this group (Smithers, 1972). Therefore, its presence in the specimen would indicate that it is a plesiomorphic character. The two-branched M in forewings is an unstable character in Psocodea, so it is risky to use it alone for adscription to a group. Considering this information, we believe that some characters present in the studied specimen point out a belonging to Psocomorpha, although it does not fit diagnosis of any family, so it might correspond to a stem branch to Psocomorpha. Its poor preservation and taphonomic artefacts explain the challenging taxonomic identification. We decide not to name new taxa based on this specimen. Based on the uncommon combination of characters and its striking similarity to the wing venation to the genus *Scottiella* (living in Seychelles islands), we prefer to describe it as morphotype Ariño, as it can be used for comparison with other better preserved Cretaceous specimens. The finding of specimens with similar habitus may help to determine the phylogenetic placement of the barklouse morphotype Ariño.

To date, only four Cretaceous psocomorphan species have been described (Vishniakova, 1975; Azar et al., 2015; Yoshizawa and Yamamoto, 2021): *Burmesopsocus lienhardi* Yoshizawa, 2021 (Homilopsocidea *incertae sedis*) from Cenomanian Burmese amber, and *Mesopsocoides dupei* Azar, Nel and Perrichot, 2015 (Mesopsocidae) from Cenomanian–Turonian Vendean amber, *Cretapsocus capillatus* Vishniakova, 1975 (*incertae sedis*) and *Archaelachesis granulosa* Vishniakova, 1975 (Lachesillidae), both from Santonian Yantardakh amber. Considering these species, the morphotype Ariño shares some characters with *C. capillatus*, such as the forewing with M two-branched, hind wing with crossvein rs-m and unbranched M, two-segmented tarsi, and preapical tooth absent (Vishniakova, 1975). Nevertheless, *C. capillatus* has a densely setose margin and membrane on both wings, Sc is absent on the forewing, Rs and M are fused for a length, the areola postica is elongate, and there is no nodulus (Vishniakova, 1975). Thus, the morphotype Ariño is clearly different to all the previously described Cretaceous psocomorphans.

4. Discussion

The known diversity of the Cretaceous psocids has rapidly increased in recent years following the description of new taxa mainly from Burmese amber (Myanmar), but also from other ambers around the world, such as Canadian, Spanish, French, Lebanese, and Taimyr (Russia) ambers (Azar et al., 2015; Cockx et al., 2020; Álvarez-Parra et al., 2020b, 2022; Hakim et al., 2021, 2022). Interestingly, the suborder Trogiomorpha accounts for most of the Cretaceous psocid species, whereas today it is the least diverse (Álvarez-Parra et al., 2022). To date, Troctomorpha encompasses 25 Cretaceous species. The study of Cretaceous troctomorphans sheds light on the origin of the parasitic lice, which may have occurred around 115 Ma, during the Early Cretaceous (de Moya et al., 2021). Until now, only one fossil louse species has been identified, *Megamenopon rasnitsyni* Wappler, Smith and Dalgleish, 2004 (Menoponidae), from the Eocene Eckfeld Maar in Germany (Wappler et al., 2004; Dalgleish et al., 2006). Another undescribed fossil louse has been reported from the Pleistocene Locality 49 of the Ziegler Reservoir fossil site in the USA (Elias, 2014). Lice-like insects, supposedly ectoparasitic, have turned out to be hemipterans unrelated to Phthiraptera (Grimaldi and Vea, 2021). The psocid family most closely related to the parasitic lice is Liposcelididae (de Moya et al., 2021), which has a fossil record with representatives from the Cretaceous, Eocene, and Miocene (Nel et al., 2004; Grimaldi and Engel, 2006). The origin of ectoparasitism in Psocodea remains obscure, based on differences between the anatomic morphology of parasitic and non-parasitic members of the order (de Moya et al., 2021). Nonetheless, the study of dinosaur feathers and associated entomofauna from Cretaceous ambers may yield key information about the general morphotype of the ancient lice, similarly to other groups of parasitic arthropods (e.g., Peñalver et al., 2017). Furthermore, it is expected that new 'transitional' specimens will be described from Cretaceous ambers, showing a combination of characters typical of different families, such as the recently described genus *Burmempheria* (Trogiomorpha: †Empheriidae) shows characters typical of †Archaeatropidae and †Empheriidae (Li et al., 2020), and has led to synonymise the first family under the second one (Li et al., 2022). These taxa, although challenging to place systematically, help to understand the relationships between the psocid families and the evolution of the group during the Cretaceous.

The description of *Azarpsocus anjana* sp. nov. in Manicapsocidae and *Burmacompsocus ojancano* sp. nov. in Compsocidae expands our knowledge of the early diversification and palaeogeographical distribution of these families. They are the first Cretaceous representatives of their corresponding families to be found in an amber other than the rich in bioinclusions Cenomanian Burmese amber. Furthermore, they are also the oldest records of both Manicapsocidae and Compsocidae, providing new calibration points for phylogenetic analyses. The Manicapsocidae correspond to eight extant species mainly found in South and Central America and an additional species from south-eastern inland Africa (Mockford, 1996; Hakim et al., 2020). The fossil record of the family includes six Cretaceous species in four genera (adding *A. anjana* sp. nov.) and two Eocene species in two genera (Nel et al., 2005; Hakim et al., 2020). The genus *Burmacompsocus* was highly diverse during the Cretaceous, containing five species (including *B. ojancano* sp. nov.). Interestingly, the family Compsocidae includes six Cretaceous species, but only two extant species, which inhabit Central America (Mockford, 1967; Azar et al., 2016). Thus, it is plausible that these families showed a high diversity and wide distribution during the Cretaceous and then underwent vicariance and extinction processes, probably due to niche competition with the more derived psocomorphans, relegating them to the current restricted distribution, similarly to other Cretaceous trogiomorphan families (Álvarez-Parra et al., 2022).

The Burmese amber, containing specimens belonging to Manicapsocidae and Compsocidae, is related to resiniferous trees from

Table 1
Co-occurrence of barklice (Psocodea) genera found in Spanish ambers and in other Cretaceous ambers. Suborders are in blue, families are in green, and genera are in yellow.

Taxon	Lebanon	Spain	France	Myanmar	USA	Russia	Canada
Trogiomorpha	X	X	X	X	X	X	X
†Empheriidae	X	X	X	X	X	X	
Archaeatropos	X	X					
Empheropsocus		X					
Libanoglaris	X	X					
Preempheria		X					
Troctomorpha	X	X	X	X		X	X
Compsocidae		X		X			
Burmacompsocus		X		X			
Manicapsocidae		X		X			
Azarpsocus		X		X			
Manicapsocidus		X					
Psocomorpha		X?	X	X		X	

the Burma Terrane, which was a near-equatorial Tethyan island during the mid-Cretaceous, explaining the high degree of endemism (Westerweel et al., 2019). It is thought to have been located between the Indian and Australian blocks in East Gondwana during the Early Jurassic and then displaced northward during the Late Jurassic–Early Cretaceous (Heine et al., 2004; Westerweel et al., 2019). Nonetheless, the proposed hypothesis on the Gondwanan origin of part of the Burmese amber biota is controversial (Clarke et al., 2019; Peris and Jelínek, 2020; Morley et al., 2021; Chitimia-Dobler et al., 2022). The lack of fossil manicapsocids and compsocids in other Gondwanan ambers would discard their Gondwanan origin. Consequently, the migration of these psocid families from south-eastern Asia to the Burma Terrane cannot be ruled out. Therefore, the discovery of new troctomorphans in African (Bouju and Perrichot, 2020) or Australian (Stilwell et al., 2020) Cretaceous ambers would help to determine the evolutionary origin of these groups. Interestingly, although the Iberia Island was geographically close to Laurasia, the psocid fauna from Spanish amber seems to be more similar to that from Lebanese and Burmese ambers (Table 1). The genera *Archaeatropos* and *Libanoglaris* (both within †Empheriidae in Trogiomorpha) are also present in Barremian Lebanese amber (Álvarez-Parra et al., 2022), while the genera studied here, *Azarpsocus* and *Burmacompsocus*, are found in Cenomanian Burmese amber. Thus, the psocid fauna of Iberia (Albian in age) shares more similarities with the fauna from these distant amber deposits than with that from the geographically closer French amber (Cenomanian). In the Albian, resiniferous forests were distributed throughout north and eastern Iberia, whereas during the Cenomanian, the resiniferous forests were present in the southern and western Armorica-French Central Massif, both regions separated by an oceanic strait of around a few hundred kilometres (Álvarez-Parra et al., 2022, figure 1). Thus, a certain similarity between psocid faunas would be expected. The differences might be explained by the palaeobarrier that this strait represented, maybe reinforced by the oceanic currents connecting the Tethys Sea and the North Atlantic Ocean, as occurred since the Miocene in the Channel of Mozambique, between Africa and Madagascar (Delclòs et al., 2020). Nevertheless, further study is required of the reasons for these anomalous relations among psocid faunas, following the description of new specimens from these provenances. The co-occurrence of insect genera from Lebanese or Burmese ambers with Spanish amber has been noted previously for groups such as springtails, beetles, wasps, and dipterans (e.g., Ortega-Blanco et al., 2011; Pérez-de la Fuente et al., 2011; Peris et al., 2014, 2016; Sánchez-García and Engel, 2016; Arillo et al., 2018; Santer et al., 2022), whereas there are few similarities between the Cretaceous insect faunas from Spanish amber and French amber (Peris et al., 2016). A study of the Spanish Cretaceous palynoflora has also revealed differences with that from the upper Albian–middle Cenomanian of western France (Barrón et al., 2015). The palaeoenvironmental and palaeoclimatic conditions and the botanical assemblages of the amber deposits together with the Cretaceous palaeogeography might help to explain the differences and similarities between the arthropod faunas inhabiting resiniferous forests (Peris et al., 2016). As mentioned above, the flow of oceanic currents around Iberia during the mid-Cretaceous might have facilitated or hindered arthropod faunal displacements through some areas. The displacement of barklice through oceanic or wind currents has been suggested for explaining the current biogeography of this group (Mockford, 2012; Álvarez-Parra and Nel, 2022).

Psocomorpha is the most diverse psocid suborder today, although its representatives are almost unknown from the Cretaceous (Yoshizawa and Yamamoto, 2021; Álvarez-Parra et al., 2022). The morphotype Ariño described here might belong to Psocomorpha. Its poor preservation prevents the assignment to a known family, although it seems to share similarities regarding wing venation, with the pseudocaeciliid genus *Scotiella*, nowadays living in islands far from continental masses (Enderlein, 1931). Therefore, despite the antiquity, the wing venation of morphotype Ariño seems to be somewhat derived, although the presence of vein 2A in forewing would indicate the contrary, being a plesiomorphic stem representative to Psocomorpha. The genus *Paramesopsocus* (known by a Late Jurassic species and a Barremian species) also shows vein 2A (Azar et al., 2008), although the rest of forewing and hind wing venations are different to those of the studied specimen (Azar et al., 2008); this genus was firstly assigned to Psocomorpha (Azar et al., 2008), and later transferred to Electrentomidae (Troctomorpha) (Mockford et al., 2013). The only known psocomorphan from Burmese amber, *Burmesopsocus lienhardi*, shows derived characters for Psocomorpha (Yoshizawa and Yamamoto, 2021). This information is interesting, as one would expect to find 'basal' psocomorphans, such as Archipsocidae (de Moya et al., 2021), in Cretaceous ambers, whereas the oldest known records of this family are from the Eocene (Nel et al., 2005). As Yoshizawa and Yamamoto (2021) have noted, it is likely that new psocomorphan specimens will be described from Cretaceous ambers, revealing the early evolution of the group and providing insights into its origin.

5. Conclusions

The description of two new species and a new morphotype in Albian Spanish amber supports the idea that the barklice showed relatively high diversity during the Cretaceous. The barklice fauna of resiniferous forests in Iberia was diverse, with the psocodean suborders Trogiomorpha and Troctomorpha present and possibly also Psocomorpha, accounting for eight species within seven genera. Information about their palaeobiology remains poor, but they probably had a similar lifestyle to the extant representatives of the group, inhabiting forest litter and the bark of the trunk and branches of resiniferous trees. More globally, barklice fauna was diverse during the Early Cretaceous, with the oldest representatives of several extant families (such as Prionoglarididae, Manicapsocidae, Compsocidae, Pachytroctidae, and Sphaeropsocidae), but also some extinct families (such as †Empheriidae). Unfortunately, while the Eocene psocid fauna is relatively well known thanks to the Oise, Baltic, and Rovno ambers, our knowledge of the latest Cretaceous and Paleocene psocids is very poor. Bridging this crucial gap will require considerable research effort in the coming years and investigation into new amber outcrops and Konservat-Lagerstätten of continental compression rocks covering this interval, which comprises the Cretaceous–Cenozoic crisis. The exact impact of this crisis on the Psocodea remains virtually unknown.

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References

Alcalá, L., Espílez, E., Mampel, L., Kirkland, J.I., Ortiga, M., Rubio, D., González, A., Ayala, D., Cobos, A., Royo-Torres, R., Gascó, F., Pesquero, M.D., 2012. A new Lower Cretaceous vertebrate bonebed near Ariño (Teruel, Aragón, Spain); found and managed in a joint collaboration between a mining company and a palaeontological park. Geoheritage 4 (4), 275–286. https://doi.org/10.1007/s12371-012-0068-y.

Álvarez-Parra, S., Nel, A., 2022. A new genus of setose-winged barklice (Psocodea: Trogiomorpha: Lepidopsocidae) from the Eocene amber of Oise with notes on the biogeography of Thylacellinae. Historical Biology 1–10. https://doi.org/10.1080/08912963.2022.2081566.

Álvarez-Parra, S., Delclòs, X., Solórzano-Kraemer, M.M., Alcalá, L., Peñalver, E., 2020a. Cretaceous amniote integuments recorded through a taphonomic process unique to resins. Scientific Reports 10, 19840. https://doi.org/10.1038/s41598-020-76830-8.

Álvarez-Parra, S., Peñalver, E., Nel, A., Delclòs, X., 2020b. The oldest representative of the extant barklice genus *Psyllipsocus* (Psocodea: Trogiomorpha: Psyllipsocidae) from the Cenomanian amber of Myanmar. Cretaceous Research 113, 104480. https://doi.org/10.1016/j.cretres.2020.104480.

Álvarez-Parra, S., Pérez-de la Fuente, R., Peñalver, E., Barrón, E., Alcalá, L., Pérez-Cano, J., Martín-Closas, C., Trabelsi, K., Meléndez, N., López Del Valle, R., Lozano, R.P., Peris, D., Rodrigo, A., Sarto i Monteys, V., Bueno-Cebollada, C.A., Menor-Salván, C., Philippe, M., Sánchez-García, A., Peña-Kairath, C., Arillo, A., Espílez, E., Mampel, L., Delclòs, X., 2021. Dinosaur bonebed amber from an original swamp forest soil. eLife 10, e72477. https://doi.org/10.7554/eLife.72477.

Álvarez-Parra, S., Peñalver, E., Nel, A., Delclòs, X., 2022. New barklice (Psocodea: Trogiomorpha) from Lower Cretaceous Spanish amber. Papers in Palaeontology 8 (3), e1436. https://doi.org/10.1002/spp2.1436.

Arillo, A., Blagoderov, V., Peñalver, E., 2018. Early Cretaceous parasitism in amber: a new species of *Burmazelmira* fly (Diptera: Archizelmiridae) parasitized by a *Leptus* sp. mite (Acari, Erythraeidae). Cretaceous Research 86, 24–32. https://doi.org/10.1016/j.cretres.2018.02.006.

Arillo, A., Subías, L.S., Álvarez-Parra, S., 2022. First fossil record of the oribatid family Liacaridae (Acariformes: Gustavioidea) from the lower Albian amber-bearing site of Ariño (eastern Spain). Cretaceous Research 131, 105087. https://doi.org/10.1016/j.cretres.2021.105087.

Azar, D., Nel, A., 2011. The oldest psyllipsocid booklice, in Lower Cretaceous amber from Lebanon (Psocodea, Trogiomorpha, Psocathropetae, Psyllipsocidae). ZooKeys 130, 153–165. https://doi.org/10.3897/zookeys.130.1430.

Azar, D., Hajar, L., Indary, C., Nel, A., 2008. Paramesopsocidae, a new Mesozoic psocid family (Insecta: Psocodea “Psocoptera”: Psocomorpha). Annales de la Société Entomologique de France 44 (4), 459–470. https://doi.org/10.1080/00379271.2008.10697581.

Azar, D., Nel, A., Perrichot, V., 2015. Diverse barklice (Psocodea) from Late Cretaceous Vendean amber. Paleontological Contributions 2014 (10C), 9–15. https://doi.org/10.17161/PC.1808.15983.

Azar, D., Hakim, M., Huang, D., 2016. A new compsocid booklouse from the Cretaceous amber of Myanmar (Psocodea: Troctomorpha: Amphientometae: Compsocidae). Cretaceous Research 68, 28–33. https://doi.org/10.1016/j.cretres.2016.08.003.

Azar, D., Hakim, M., Huang, D., Cai, C., Nel, A., 2017. New fossil booklice from the Cretaceous amber of Myanmar (Psocodea: Troctomorpha: Amphientometae: Manicapsocidae). Cretaceous Research 70, 8–14. https://doi.org/10.1016/j.cretres.2016.09.013.

Badonnel, A., 1967. Psocoptères édaphiques du Chili (2e note). Biologie de l'Amérique australe 3, 541–585.

Banks, N., 1930. Some new Neotropical neuropteroid insects. Psyche 37, 183–191. https://doi.org/10.1155/1930/89823.

Barrón, E., Peyrot, D., Rodríguez-López, J.P., Meléndez, N., López Del Valle, R., Najarro, M., Rosales, I., Comas-Rengifo, M.J., 2015. Palynology of Aptian and upper Albian (Lower Cretaceous) amber-bearing outcrops of the southern margin of the Basque-Cantabrian basin (northern Spain). Cretaceous Research 52, 292–312. https://doi.org/10.1016/j.cretres.2014.10.003.

Baz, A., Ortuño, V.M., 2000. Archaeatropidae, a new family of Psocoptera from the Cretaceous amber of Alava, Northern Spain. Annals of the Entomological Society of America 93 (3), 367–373. https://doi.org/10.1603/0013-8746(2000)093[0367:AANFOP]2.0.CO;2.

Baz, A., Ortuño, V.M., 2001a. A new electrentomoid psocid (Psocoptera) from the Cretaceous amber of Alava (Northern Spain). Deutsche Entomologische Zeitschrift 48, 27–32. https://doi.org/10.1002/dez.200100004.

Baz, A., Ortuño, V.M., 2001b. New genera and species of empheriids (Psocoptera: Empheriidae) from the Cretaceous amber of Alava, northern Spain. Cretaceous Research 22 (5), 575–584. https://doi.org/10.1006/cres.2001.0275.

Bouju, V., Perrichot, V., 2020. A review of amber and copal occurrences in Africa and their paleontological significance. BSGF-Earth Sciences Bulletin 191 (1), 17. https://doi.org/10.1051/bsgf/2020018.

Casasola González, J.A., 2006. Phylogenetic relationships of the genera of Epipsocetae (Psocoptera: Psocomorpha). Zootaxa 1194 (1), 1–32. https://doi.org/10.11646/zootaxa.1194.1.1.

Chitimia-Dobler, L., Dunlop, J.A., Pfeffer, T., Würzinger, F., Handschuh, S., Mans, B.J., 2022. Hard ticks in Burmese amber with Australasian affinities. Parasitology 1–15. https://doi.org/10.1017/S0031182022001585.

Clarke, D.J., Limaye, A., McKenna, D.D., Oberprieler, R.G., 2019. The weevil fauna preserved in Burmese amber—snapshot of a unique, extinct lineage (Coleoptera: Curculionoidea). Diversity 11 (1), 1. https://doi.org/10.3390/d11010001.

Cockerell, T.D.A., 1916. Insects in Burmese amber. American Journal of Science 42, 135–138. https://doi.org/10.2475/ajs.s4-42.248.135.

Cockx, P., McKellar, R., Tappert, R., Vavrek, M., Muehlenbachs, K., 2020. Bonebed amber as a new source of paleontological data: the case of the Pipestone Creek deposit (Upper Cretaceous), Alberta, Canada. Gondwana Research 81, 378–389. https://doi.org/10.1016/j.gr.2019.12.005.

Corral, J.C., López Del Valle, R., Alonso, J., 1999. El ámbar cretácico de Álava (Cuenca Vasco-Cantábrica, norte de España). Su colecta y preparación. Estudios del Museo de Ciencias Naturales de Álava 14, 7–21.

Dalgleish, R.C., Palma, R.L., Price, R.D., Smith, V.S., 2006. Fossil lice (Insecta: Phthiraptera) reconsidered. Systematic Entomology 31 (4), 648–651. https://doi.org/10.1111/j.1365-3113.2006.00342.x.

Delclòs, X., Peñalver, E., Ranaivosoa, V., Solórzano-Kraemer, M.M., 2020. Unravelling the mystery of "Madagascar copal": age, origin and preservation of a Recent resin. PLoS One 15 (5), e0232623. https://doi.org/10.1371/journal.pone.0232623.

de Moya, R.S., Yoshizawa, K., Walden, K.K., Sweet, A.D., Dietrich, C.H., Kevin, P.J., 2021. Phylogenomics of parasitic and nonparasitic lice (Insecta: Psocodea): combining sequence data and exploring compositional bias solutions in next generation data sets. Systematic Biology 70, 719–738. https://doi.org/10.1093/sysbio/syaa075.

Elias, S.A., 2014. Environmental interpretation of fossil insect assemblages from MIS 5 at Ziegler Reservoir, Snowmass Village, Colorado. Quaternary Research 82 (3), 592–603. https://doi.org/10.1016/j.yqres.2014.01.005.

Enderlein, G., 1911. Die Fossilen Copeognathen und ihre Phylogenie. Palaeontographica 58, 279–360.

Enderlein, G., 1926. Die Copeognathen-Fauna Javas. Zoologische Mededeelingen 9, 50–70.

Enderlein, G., 1931. Die Copeognathen Fauna der Seychellen. Transactions of the Linnean Society of London 2nd Series Zoology 19 (2), 207–240. https://doi.org/10.1111/j.1096-3642.1931.tb00127.x.

García-Mondéjar, J., 1982. Aptiense y Albiense. In: Alonso, A., Arias, C., García, A., Mas, R., Rincón, R., Vilas, L. (Eds.), El Cretácico de España. Editorial Universidad Complutense de Madrid, Madrid, pp. 63–84.

Grimaldi, D., Engel, M.S., 2006. Fossil Liposcelididae and the lice ages (Insecta: Psocodea). Proceedings of the Royal Society B: Biological Sciences 273 (1586), 625–633. https://doi.org/10.1098/rspb.2005.3337.

Grimaldi, D.A., Vea, I.M., 2021. Insects with 100 million-year-old dinosaur feathers are not ectoparasites. Nature Communications 12, 1469. https://doi.org/10.1038/s41467-021-21751-x.

Hakim, M., Azar, D., Huang, D., 2020. A unique manicapsocid (Psocodea: Amphientometae) from the mid-Cretaceous Burmese amber. Cretaceous Research 107, 104278. https://doi.org/10.1016/j.cretres.2019.104278.

Hakim, M., Huang, D.-Y., Azar, D., 2021. New fossil psocids from Cretaceous Siberian ambers (Psocodea: Trogiomorpha: Atropetae). Palaeoentomology 4 (2), 186–198. https://doi.org/10.11646/PALAEOENTOMOLOGY.4.2.8.

Hakim, M., Huang, D.-Y., Azar, D., 2022. Earliest record of Prionoglarididae from the Lower Cretaceous Lebanese amber (Psocodea; Trogiomorpha). Cretaceous Research 132, 105121. https://doi.org/10.1016/j.cretres.2021.105121.

Heine, C., Müller, R.D., Gaina, C., Clift, P., Kuhnt, W., Wang, P., Hayes, D., 2004. Reconstructing the lost eastern Tethys ocean basin: convergence history of the SE Asian margin and marine gateways. Continent-ocean interactions within East Asian Marginal Seas. Geophysical Monograph Series 149, 37–54. https://doi.org/10.1029/149GM03.

Hennig, W., 1966. Phylogenetic Systematics. University of Illinois Press, Champaign, p. 263.

Johnson, K.P., Dietrich, C.H., Friedrich, F., Beutel, R.G., Wipfler, B., Peters, R.S., Allen, J.M., Petersen, M., Donath, A., Walden, K.K.O., Kozlov, A.M., Podsiadlowski, L., Mayer, C., Meusemann, K., Vasilikopoulos, A., Waterhouse, R.M., Cameron, S.L., Weirauch, C., Swanson, D.R., Percy, D.M., Hardy, N.B., Terry, I., Liu, S., Zhou, X., Misof, B., Robertson, H.M., Yoshizawa, K., 2018. Phylogenomics and the evolution of hemipteroid insects. Proceedings of the National Academy of Sciences 115 (50), 12775–12780. https://doi.org/10.1073/pnas.1815820115.

Jouault, C., Yoshizawa, K., Hakim, M., Huang, D., Nel, A., 2021. New psocids (Psocodea: Prionoglarididae, Psyllipsocidae) from Cretaceous Burmese amber deposits. Cretaceous Research 126, 104890. https://doi.org/10.1016/j.cretres.2021.104890.

Li, S., Wang, Q., Ren, D., Yao, Y., 2020. New genus and species of Empheriidae (Psocodea: Trogiomorpha) from mid-Cretaceous amber of northern Myanmar. Cretaceous Research 110, 104421. https://doi.org/10.1016/j.cretres.2020.104421.

Li, S., Yoshizawa, K., Wang, Q., Ren, D., Bai, M., Yao, Y., 2022. New genus and species of† Empheriidae (Insecta: Psocodea: Trogiomorpha) and their implication for the phylogeny of infraorder Atropetae. Frontiers in Ecology and Evolution 10, 907903. https://doi.org/10.3389/fevo.2022.907903.

Liang, F., Liu, X., 2021. A new species of *Psyllipsocus* (Psocodea: Trogiomorpha: Psyllipsocidae) from the mid-Cretaceous amber of Myanmar. Zootaxa 5072 (1), 81–87. https://doi.org/10.11646/zootaxa.5072.1.9.

Maheu, A., Nel, A., 2020. A new fossil booklouse (psocodea: Troctomorpha: Amphientometae: Manicapsocidae) from the mid-Cretaceous amber of northern Myanmar. Cretaceous Research 106, 104222. https://doi.org/10.1016/j.cretres.2019.104222.

Mas, R., García, A., Salas, R., Meléndez, A., Alonso, A., Aurell, M., Bádenas, B., Benito, M.I., Carenas, B., García-Hidalgo, J.F., Gil, J., Segura, M., 2004. Segunda fase de rifting: Jurásico Superior-Cretácico Inferior. In: Vera, J.A. (Ed.), Geología de España. Sociedad Geológica de España and Instituto Geológico y Minero de España, Madrid, pp. 503–551.

Mockford, E.L., 1967. The electrentomoid Psocids (Psocoptera). Psyche 74, 118–163. https://doi.org/10.1155/1967/862560.

Mockford, E.L., 1993. North American Psocoptera (Insecta). Sandhill Crane Press, Gainesville, p. 455.

Mockford, E.L., 1996. Character analysis of the Western Hemisphere genera of family Manicapsocidae (Psocoptera): genus *Epitroctes* reinstated with descriptions of four new species. Insecta Mundi 10, 169–180.

Mockford, E.L., 2012. Aspects of the biogeography of North American Psocoptera (Insecta). In: Stevens, L. (Ed.), Global Advances in Biogeography. InTech, Rijeka and Shanghai, pp. 307–328.

Mockford, E.L., Lienhard, C., Yoshizawa, K., 2013. Revised classification of 'Psocoptera' from Cretaceous amber, a reassessment of published information. Insecta Matsumurana New series 69, 1–26.

Morley, C.K., Chantraprasert, S., Kongchum, J., Chenoll, K., 2021. The West Burma Terrane, a review of recent paleo-latitude data, its geological implications and constraints. Earth-Science Reviews 220, 103722. https://doi.org/10.1016/j.earscirev.2021.103722.

Najarro, M., Peñalver, E., Rosales, I., Pérez-de la Fuente, R., Daviero-Gómez, V., Gómez, B., Delclós, X., 2009. Unusual concentration of Early Albian arthropod-bearing amber in the Basque-Cantabrian Basin (El Soplao, Cantabria, Northern Spain): palaeoenvironmental and palaeobiological implications. Geologica Acta 7 (3), 363–388. https://doi.org/10.1344/105.000001443.

Nel, A., Waller, A., 2007. The first fossil Compsocidae from Cretaceous Burmese amber (Insecta, Psocoptera, Troctomorpha). Cretaceous Research 28, 1039–1041. https://doi.org/10.1016/j.cretres.2007.02.002.

Nel, A., De Ploëg, G., Azar, D., 2004. The oldest Liposcelididae in the lowermost Eocene amber of the Paris Basin (Insecta: Psocoptera). Geologica Acta 2 (1), 31–36.

Nel, A., Prokop, J., De Ploëg, G., Millet, J., 2005. New Psocoptera (Insecta) from the lowermost Eocene amber of Oise, France. Journal of Systematic Palaeontology 3 (4), 371–391. https://doi.org/10.1017/S1477201905001598.

Nel, A., Roques, P., Nel, P., Prokin, A.A., Bourgoin, T., Prokop, J., Szwedo, J., Azar, D., Desutter-Grandcolas, L., Wappler, T., Garrouste, R., Coty, D., Huang, D., Engel, M.S., Kirejtshuk, A.G., 2013. The earliest known holometabolous insects. Nature 503 (7475), 257–261. https://doi.org/10.1038/nature12629.

New, T.R., 1987. Biology of the Psocoptera. Oriental Insects 21 (1), 1–109. https://doi.org/10.1080/00305316.1987.11835472.

New, T.R., Lienhard, C., 2007. The Psocoptera of Tropical South-east Asia. In: National Museum of Natural History Naturalis. Brill, Leiden, p. 290.

Ngô-Muller, V., Garrouste, R., Nel, A., 2020. Small but important: a piece of mid-Cretaceous Burmese amber with a new genus and two new insect species (Odonata: Burmaphlebiidae & 'Psocoptera': Compsocidae). Cretaceous Research 110, 104405. https://doi.org/10.1016/j.cretres.2020.104405.

Ortega-Blanco, J., Delclòs, X., Engel, M.S., 2011. Diverse stigmaphronid wasps in Early Cretaceous amber from Spain (Hymenoptera: Ceraphronoidea: Stigmaphronidae). Cretaceous Research 32 (6), 762–773. https://doi.org/10.1016/j.cretres.2011.05.004.

Pearman, J.V., 1936. The taxonomy of the Psocoptera: preliminary sketch. Proceedings of the Royal Entomological Society of London (B) 5, 58–62. https://doi.org/10.1111/j.1365-3113.1936.tb00596.x.

Peñalver, E., Nel, A., Martínez-Delclòs, X., 1996. Insectos del Mioceno inferior de Ribesalbes (Castellón, España). Paleoptera y Neoptera poli- y paraneoptera. Treballs del Museu de Geologia de Barcelona 5, 15–95.

Peñalver, E., Arillo, A., Delclòs, X., Peris, D., Grimaldi, D.A., Anderson, S.R., Nascimbene, P.C., Pérez-de la Fuente, R., 2017. Ticks parasitised feathered dinosaurs as revealed by Cretaceous amber assemblages. Nature Communications 8, 1924. https://doi.org/10.1038/s41467-017-01550-z.

Pérez-de la Fuente, R., Delclòs, X., Peñalver, E., Arillo, A., 2011. Biting midges (Diptera: Ceratopogonidae) from the Early Cretaceous El Soplao amber (N Spain). Cretaceous Research 32 (6), 750–761. https://doi.org/10.1016/j.cretres.2011.05.003.

Peris, D., Jelínek, J., 2020. Syninclusions of two new species of short-winged flower beetle (Coleoptera: Kateretidae) in mid-Cretaceous Kachin amber (Myanmar). Cretaceous Research 106, 104264. https://doi.org/10.1016/j.cretres.2019.104264.

Peris, D., Chatzimanolis, S., Delclòs, X., 2014. Diversity of rove beetles (Coleoptera: Staphylinidae) in Early Cretaceous Spanish amber. Cretaceous Research 48, 85–95. https://doi.org/10.1016/j.cretres.2013.11.008.

Peris, D., Ruzzier, E., Perrichot, V., Delclòs, X., 2016. Evolutionary and paleobiological implications of Coleoptera (Insecta) from Tethyan-influenced Cretaceous ambers. Geoscience Frontiers 7 (4), 695–706. https://doi.org/10.1016/j.gsf.2015.12.007.

Roesler, R., 1940. Neue und wenig bekannte Copeognathengattungen. I. Zoologischer Anzeiger 129, 225–243.

Sánchez-García, A., Engel, M.S., 2016. Springtails from the Early Cretaceous amber of Spain (Collembola: Entomobryomorpha), with an annotated checklist of fossil Collembola. American Museum Novitates 2016 (3862), 1–47. https://doi.org/10.1206/3862.1.

Santer, M., Álvarez-Parra, S., Nel, A., Peñalver, E., Delclòs, X., 2022. New insights into the enigmatic Cretaceous family Spathiopterygidae (Hymenoptera: Diaprioidea). Cretaceous Research 133, 105128. https://doi.org/10.1016/j.cretres.2021.105128.

Smithers, C.N., 1972. The classification and phylogeny of the Psocoptera. Australian Museum Memoir 14, 1–349.

Smithers, C.N., 1990. Keys to the families and genera of Psocoptera (Arthropoda, Insecta). Technical Reports of the Australian Museum 2, 1–82.

Sroka, P., Nel, A., 2017. New species of Compsocidae (Insecta, Psocodea) from Cretaceous Burmese amber. Zootaxa 4320, 597–600. https://doi.org/10.11646/zootaxa.4320.3.12.

Stilwell, J.D., Langendam, A., Mays, C., Sutherland, L.J., Arillo, A., Bickel, D.J., De Silva, W.T., Pentland, A.H., Roghi, G., Price, G.D., Cantrill, D.J., Quinney, A., Peñalver, E., 2020. Amber from the Triassic to Paleogene of Australia and New Zealand as exceptional preservation of poorly known terrestrial ecosystems. Scientific Reports 10, 5703. https://doi.org/10.1038/s41598-020-62252-z.

Tibert, N.E., Colin, J.P., Kirkland, J.I., Alcalá, L., Martín-Closas, C., 2013. Lower Cretaceous nonmarine ostracodes from an Escucha Formation dinosaur bonebed in eastern Spain. Micropaleontology 59 (1), 83–91.

Vajda, V., Pesquero Fernández, M.D., Villanueva-Amadoz, U., Lehsten, V., Alcalá, L., 2016. Dietary and environmental implications of Early Cretaceous predatory dinosaur coprolites from Teruel, Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 464, 134–142. https://doi.org/10.1016/j.palaeo.2016.02.036.

Villanueva-Amadoz, U., Sender, L.M., Alcalá, L., Pons, D., Royo-Torres, R., Diez, J.B., 2015. Paleoenvironmental reconstruction of an Albian plant community from the Ariño bonebed layer (Iberian Chain, NE Spain). Historical Biology 27 (3–4), 430–441. https://doi.org/10.1080/08912963.2014.895826.

Vishniakova, V.N., 1975. Psocoptera in Late-Cretaceous insect-bearing resins from the Taimyr. Entomological Review 54, 63–75.

Wappler, T., Smith, V.S., Dalgleish, R.C., 2004. Scratching an ancient itch: an Eocene bird louse fossil. Proceedings of the Royal Society of London. Series B: Biological Sciences 271 (Suppl. 5), S255–S258. https://doi.org/10.1098/rsbl.2003.0158.

Westerweel, J., Roperch, P., Licht, A., Dupont-Nivet, G., Win, Z., Poblete, F., Ruffet, G., Swe, H.H., Thi, M.K., Aung, D.W., 2019. Burma Terrane part of the Trans-Tethyan arc during collision with India according to palaeomagnetic data. Nature Geoscience 12, 863–868. https://doi.org/10.1038/s41561-019-0443-2.

Yoshizawa, K., 2000. Redescription of *Mepleres suzukii* (Okamoto), with comments on synonymy among *Mepleres, Pseudoscottiella* and *Meniscopsocus* (Psocodea: 'Psocoptera': Pseudocaeciliidae). Entomological Science 3, 669–674. http://hdl.handle.net/2115/35638.

Yoshizawa, K., Yamamoto, S., 2021. The earliest fossil record of the suborder Psocomorpha (Insecta: Psocodea) from mid-Cretaceous Burmese amber, with description of a new genus and species. Insecta Matsumurana New series 77, 1–15.

Yoshizawa, K., Johnson, K.P., 2014. Phylogeny of the suborder Psocomorpha: congruence and incongruence between morphology and molecular data (Insecta: Psocodea: ‘Psocoptera’). Zoological Journal of the Linnean Society 171 (4), 716–731. https://doi.org/10.1111/zoj.12157.

Yoshizawa, K., Lienhard, C., Yao, I., Ferreira, R.L., 2019. Cave insects with sex-reversed genitalia had their most recent common ancestor in West Gondwana (Psocodea: Prionoglarididae: Speleketorinae). Entomological Science 22 (3), 334–338. https://doi.org/10.1111/ens.12374.